

# Conserving Bird Biodiversity

General principles and their application

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# Biodiversity – evolution, species, genes

MICHAEL W. BRUFORD

## INTRODUCTION

In many respects biodiversity, both present and past, is better understood for birds than for any other major group of organisms. This is because birds probably inspire more extreme interest in humans than all other animals (and most plants): they are often spectacular, are relatively easily observed and are usually neither too specious nor too cryptic to identify or study. Ironically, by being desirable to the collector and enigmatic and tractable to both the hobbyist and scientist, birds have helped us to document the effects of anthropogenic interference on the Earth's biodiversity during the last few hundred years in the most extraordinary detail. In birds, we benefit from an extremely rich history of scientific study, from much research of high quality in the modern era and from an enviable, though chequered, track record in conservation management. It is, however, abundantly clear that our ability to synthesise and utilise this level of knowledge will be sorely tested in the near future as we attempt to guide many avian populations through the profound environmental and biological changes that are taking place now and that will intensify in the future.

In this chapter, I will attempt to describe avian biological diversity not in the details of individual species, their distributions, status and ecological requirements, but in the context of the evolutionary history that has led to the roughly 9,000 species we have today and the broad patterns of avian diversity that we currently observe, from communities to individuals. I intend to concentrate slightly more on the role that molecular systematics and population genetics can play in this endeavour, primarily because this is not covered in detail elsewhere in the book. It will become apparent (I hope) that although we know a great deal about the history of modern birds, their taxonomy and distribution, we still lack much of the crucial information we

may need for conservation management, especially below the species level, and we urgently need to draw lessons from ongoing research in avian biodiversity and its conservation so that we may apply this knowledge to other species and contexts.

## LEVELS OF BIODIVERSITY

Biodiversity (shorthand for biological diversity) is simply a term to describe the diversity of biological entities on Earth, although it has been and continues to be applied in a huge variety of contexts and at many different levels (see Gaston 1996a). It can describe genetic diversity, morphological diversity, physiological diversity, behavioural diversity, and indeed any character that is used to mark out an individual, population or species as different from another. It is increasingly described at a variety of levels in an attempt to simplify what might at first seem an overwhelmingly complex system. A top-down hierarchy from communities to species to genes is often used (as I have done below) fully in the knowledge that it is an inadequate way to describe the way each component of biodiversity influences and interacts with the others.

### Community/ecosystem

At its broadest scale, we can attempt to characterise and understand biodiversity at the community or ecosystem level. Disentangling the relationships within and among assemblages of broad classes of species which are often unconnected by recent evolutionary history, but which may perform common or integrated functions within an ecosystem, has proved to be extremely challenging. This bewildering level of complexity remains a 'black box' for the most part, and understanding and predicting the effects of interactions on community structure in nature remains a Herculean task for ecosystem-level researchers. Nonetheless, avian community structure is relatively well understood in comparison with many groups, and the effects of anthropogenic change on community interactions have led to some interesting case studies coming to light. Avian species, although comprising only a small element of any given ecosystem, have been shown to interact in crucial ways with other species to maintain ecosystem health. As major seed dispersers and pollinators, bird species can, for example, play a vital role in maintaining plant community structure and diversity (e.g. Whitney & Smith 1998) and where species are no longer represented in such ecosystems (e.g. Cooper *et al.* 1993) major ecological changes (e.g. Smith *et al.* 1995) and chains of extinction can result. Birds play important roles as

predators, form major prey bases and engage in a wide range of apparently mutualistic (e.g. Weeks 2000) and host-parasite interactions. While it is quite clearly impossible to examine these roles in all but a small number of cases, we already know that loss of avian biodiversity, though tragic in its own right, can have much wider ramifications.

### Species

Compared with other animal and plant groups, our knowledge of avian diversity at the species level is nothing short of immense, and one might almost conclude that it is as near to complete as is necessary at the present time. New species are still occasionally being discovered, sometimes in quite spectacular fashion (Smith *et al.* 1991). However, it is generally accepted that within the near future it is possible that we will have a complete picture of extant avian species diversity. In addition, our knowledge of the geographical distribution of many species and how this has changed in the last 100–200 years is also relatively good, thanks largely to the many hobbyist birdwatchers and ornithologists throughout the world who are continually augmenting and refining this knowledge, and thanks also to the considerable number of vast and well-curated museum collections found mainly in countries with a history of ornithology and/or colonialism. This wealth of information has allowed us to document and analyse geographical patterns of diversity in birds and has enabled conservationists to estimate species diversity (*species richness*: Gaston 1996b) and to examine patterns among geographically restricted species (*endemism*: Myers *et al.* 2000). This level of information has permitted the use of birds as model species to investigate the location of biodiversity ‘hotspots’ of species-richness and endemism and potentially the establishment of a network of globally-based conservation priority areas recently refined by BirdLife International into ‘Endemic Bird Areas’ (e.g. Bibby *et al.* 1992; Stattersfield *et al.* 1998; see also Box 5.1 and Fig. 5.3).

Perhaps the most contentious problem facing species-level conservation today concerns the ongoing debate on which units of biological diversity should form the basis of conservation planning, and whereas biological species have traditionally occupied this role, increasing evidence points to the fact that this approach may poorly estimate the amount of diversity necessary for the conservation of biological units with future evolutionary potential. The rise of phylogenetic and mate recognition species concepts (see Patterson 1981; Vogler & DeSalle 1994; Kraaijeveld 2000), and even proposals to abandon species concepts in their entirety, raise serious questions about the universality of the species and its meaning in conservation

(Moritz 1994a, b; Avise & Walker 2000; Crandall *et al.* 2000; Hendry *et al.* 2000). Further, once a biological unit for conservation has been identified, the question of prioritisation arises, and here the debate continues. The relative importance of preserving distinctive species (e.g. phenotypically, behaviourally, genetically) – also known as *taxic diversity* (e.g. Vane-Wright *et al.* 1991), as opposed to evolutionarily active lineages which demonstrate evidence of ongoing diversification – also known as *evolutionary fronts* (e.g. Erwin 1991), is another factor for consideration in assigning conservation priorities. At its most extreme, an advocate might argue that prioritising taxic diversity conserves as much of our evolutionary heritage as is possible, whereas a counter-argument is that prioritising evolutionary fronts at least ensures that extant diversity has the potential for future adaptation in a rapidly changing world. It is unfortunately the case, therefore, that even when conservation biologists think they are on safe ground, philosophical and practical scientific problems abound (see below).

### Genes

Understanding the patterns and processes that generate diversity below the species level is almost as difficult as understanding interactions among species at the community level, and as a consequence it has sometimes been regarded as less important in conservation. Genetic differentiation among populations or geographic regions may manifest itself in a number of ways and taxonomists have traditionally dealt with this diversity by describing the intraspecific units of the subspecies or race. However, given the current species concept debate, defining what constitutes a subspecies or race is fraught with inconsistency and some have argued for its abandonment (e.g. Hendry *et al.* 2000). However, we are still left with the requirement to identify, protect and legislate for diversity below the species and, as a consequence, conservationists are increasingly turning to phylogenetic definitions (Ryder 1986; Moritz 1994a, b; Vogler & DeSalle 1994; Pennock & Dimmick 1997; Waples 1998), the merits of which will be discussed below.

Genetic variation, together with its determinants within populations, is also a major issue in conservation, since natural levels of gene-flow in many continental bird species have been shown to be relatively high and should therefore be maintained where possible (e.g. Merila *et al.* 1997; Smith *et al.* 1997; Fry & Zink 1998). Since variation using neutral genetic markers is expected to correlate with recent demographic changes, small and/or isolated populations can lose genetic diversity rapidly, potentially compromising their future adaptive potential (Keller *et al.* 1994, 2001; Groombridge



*et al.* 2000). Management of such populations through the maintenance of genetic diversity is a focus of much of today's 'hands-on' population management (see below).

## CURRENT PATTERNS OF AVIAN DIVERSITY

As stated previously, our knowledge of today's avian diversity is as near to being complete as it is with any group of organisms. We know, for instance, that there are between 8,600 and about 10,000 bird species on Earth (depending on whose taxonomy one follows and allowing for further discoveries). It has been guessed that since the first birds appeared 130 million years ago between 150,000 and 1,500,000 species of bird have existed (the consensus seems to be about half a million), reaching a maximum of perhaps 11,500 at any one time, possibly during the Pleistocene, 250,000 years ago (Fuller 1987; Mountfort 1988). We also have a reasonable knowledge of how present-day species are distributed across the globe, where the greatest numbers of species are found, and where they are absent (see Chapter 5). Crucially, we also know pretty accurately how many species have gone extinct in the recent past (just over 100 in the last 400 years), where those extinctions took place and often why. We also know that at least 1,000 species are presently under threat of extinction, and this number needs to be constantly revised upwards (BirdLife International 2000).

Unfortunately, our knowledge of the basic biology and life history of bird species is much sketchier than of their distribution and taxonomy, a fact that is often thrown into sharp relief when urgent conservation measures need to be taken which rely, both for management and modelling, on basic information such as clutch size, generation time, mortality rates, etc. Some information can often be found at least within the family level, and studies have taken advantage of this information to use birds as a model to study the evolution of avian life history traits and their importance in conservation and other areas (e.g. Owens *et al.* 1999; Owens & Bennett 2000a). Such analyses would, however, not be possible were it not that a reasonably robust large-scale avian phylogeny exists, mainly through the efforts of Sibley and Ahlquist in the 1970s and 1980s, culminating in their book, *Phylogeny and Classification of Birds*, published in 1990. Their phylogeny, based on DNA-DNA hybridisation data (generated by experiments on the hybridisation properties of single-copy DNA strands from different species), has proved very useful and is generally regarded as plausible for many groups. These studies have also generated a number

of interesting ideas that have subsequently been tested using what are regarded as higher resolution approaches, such as analysis of mitochondrial gene sequences. For example, Sibley *et al.* (1988) suggested that perching birds (passerines) were divisible into two genealogical groups, the Corvida (crow-like) including all crows and the Passerida, which includes nearly all Old World and North American songbirds, and seemingly supported an established idea that passerines should be subdivided into the oscines (songbirds, possessing a voice box that can learn song) and the suboscines – the mainly Neotropical group lacking these traits. Subsequent mitochondrial cytochrome *b* sequence analysis has supported these ideas (Edwards *et al.* 1991), and indeed for broad- and fine-scale phylogenetic questions mitochondrial DNA is now being used routinely to map many parts of the avian phylogeny. Recent studies involving relatively slowly evolving mitochondrial DNA sequences (especially the ribosomal RNA genes) are now being used effectively to ask some fairly fundamental questions in avian phylogenetics, whereas more rapidly evolving DNA sequences (such as the cytochrome *b* gene) have been used to resolve relationships within families (e.g. Sheldon *et al.* 1999; van Tuinen *et al.* 2000).

## THE EVOLUTION OF AVIAN DIVERSITY

It is now accepted that birds evolved from and are recognised as members of the theropod dinosaurs, and that the earliest members of class Aves appeared some 150 MYBP (i.e. Million Years Before Present – Padian & Chiappe 1998). The first fossil member, discovered from the late Jurassic (some 145 MYBP), is the well-known *Archaeopteryx*, now represented by seven skeletons. Many of the ‘avian’ features in early birds are in fact shared with their terrestrial carnivore ancestors, the dromaeosaurs, and probably evolved for reasons other than flight. However, subsequent to *Archaeopteryx*, direct flight apparatus evolved relatively rapidly as late Jurassic and early Cretaceous birds exploited their arboreal habitat and started flying to greater degrees, and a relatively diverse group of birds appeared in the Mesozoic, possibly coincident with the break-up of the continental landmasses (Hedges *et al.* 1996; Cooper *et al.* 2001).

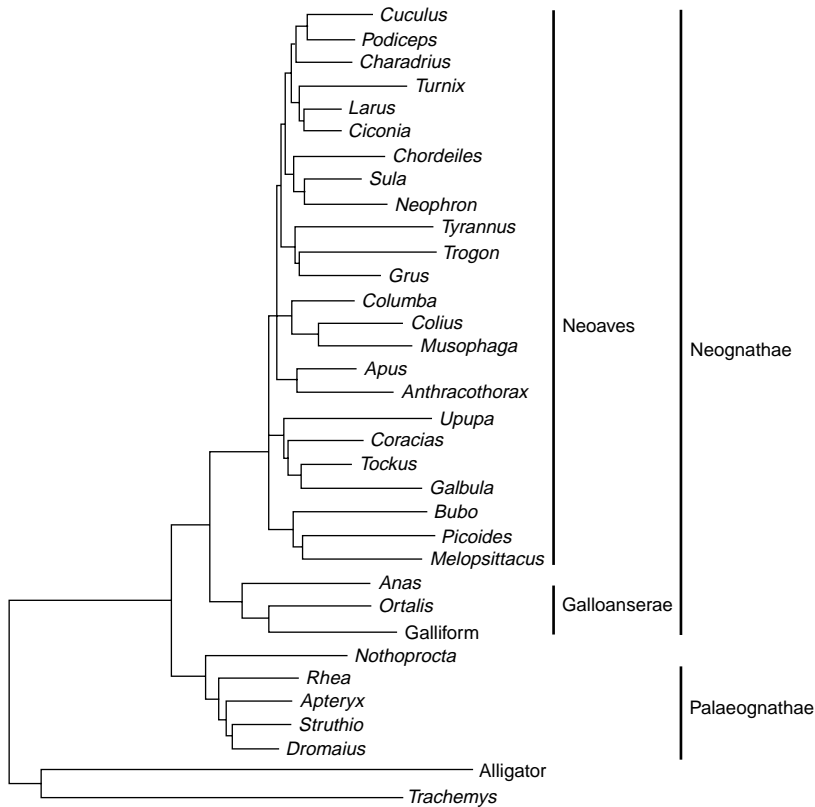
Although nearly all of these groups have no record in the Tertiary, molecular evidence dates the origin of at least 22 avian orders prior to the Cretaceous–Tertiary (K/T) boundary (Cooper & Penny 1997 – Box 1.1). This casts doubt on the dogma of a mass extinction event at that time, and argues for a rapid diversification in the ensuing 5–10 million years in the Palaeocene.

**Box 1.1.** Extant avian orders and lineages within them where sequence data estimates an origin pre-dating the K/T boundary (adapted from Cooper & Penny 1997).

Order	Number of lineages
Ratites	3
Tinamiformes	1
Galliformes	2
Anseriformes	1
Psittaciformes	3
Pelecaniformes	2
Charadriiformes	1
Passeriformes	1
Strigiformes	1
Falconiformes	1
Threskiorniformes	1
Gruiformes	1
Gaviiformes	1
Podicipediformes	1
Procellariiformes	2

Recent evidence from mitochondrial ribosomal RNA sequences (Van Tuinen *et al.* 2000) has re-contextualised the evolution of the major lineages within modern birds (Neornithes) (see Fig. 1.1), reaffirming the position of the ratites and tinamous (Palaeognathae) as the most basal lineage, followed by the ducks and Galliformes (Galloanserae) and with the Passeriformes (perching birds) as a monophyletic, derived group. This suggests that the ancestral neornithe was a large-bodied terrestrial species - a group sparsely represented in the fossil record, and divides modern birds into three major evolutionary groups. Debate remains, however, and evidence from the work of Mindell *et al.* (1999) and Härlid *et al.* (1999) even suggests that the Passeriformes may have preceded both other groups.

The arrival of convenient molecular approaches for the semi-automated analysis of long lengths of highly informative DNA sequences in extant and sometimes extinct birds (e.g. Sheldon *et al.* 1999; Omland *et al.* 2000; Cooper *et al.* 2001) has enabled a growing avian molecular phylogeny to accumulate, as current issues of journals such as *Molecular Phylogenetics and Evolution*, *Auk* and *Ibis* will testify. Unfortunately, and despite the well-documented sampling problems of inferring evolutionary events from



**Fig. 1.1.** Phylogenetic tree of modern birds based on nuclear and mitochondrial ribosomal genes. (From Van Tuinen *et al.* 2000.)

single genes, most phylogenies are based on a single gene (the mitochondrial cytochrome *b* gene) and often on fragments of that gene. The result is a rapidly expanding sequence database (Mindell 1997) with currently over 3,500 avian accessions accessible in *Genbank*, the global sequence database. This potentially allows comparisons among data sets and the construction of even larger phylogenies. However, more effort on sequencing alternative, independent, informative sequences is potentially crucial if phylogenetic hypotheses resulting from cytochrome *b* sequences are to be tested further.

It is, however, beyond question that the most pervasive influence on avian diversity in recent times has been anthropogenic (Temple 1986; Mountfort 1988; Caughley & Gunn 1996). A large proportion of birds that either have gone extinct since 1600 or are on the verge of extinction now are found on oceanic islands where they are endemic, and both the proximate

and ultimate reasons for this are well documented (Temple 1986): nearly all involve the introduction of alien species, habitat loss or over-harvesting, or a combination of these factors. The continuing pressures on avian populations across the globe mean that reduction in avian diversity is likely to continue apace, and the proportion of threatened species living on islands may decline as a result, since islands contain relatively few species that can become extinct in comparison with those in continental regions.

### SPECIES CONCEPTS, MOLECULES AND CONSERVATION

Geographical correlates of avian species diversity are becoming increasingly well understood and have led directly to a number of proposals regarding the establishment of a network of protected areas, as described in Chapter 5. These ideas have provoked much discussion (e.g. T.B. Smith *et al.* 1993) and the merits of conserving present-day patterns of species diversity, and the incorporation of a more detailed understanding of their evolutionary and ecological determinants, lie at the heart of this debate (e.g. Crandall *et al.* 2000). Incorporating intraspecific diversity into protected area conservation is an issue which is only now beginning to be addressed (see below); however, the role of species and other taxonomic definitions in conservation planning is also contentious, especially the concept of the Evolutionarily Significant Unit, which is increasingly replacing the species and subspecies as the fundamental unit for conservation management and prioritisation (e.g. Tarr & Fleischer 1999; Zink *et al.* 2000; see above).

The definition of Evolutionarily Significant Units (ESU) for conservation, introduced by Ryder (1986), has sparked much discussion on the merits and practical approaches of identifying them (e.g. Pennock & Dimmick 1997; Waples 1998). A variety of methods have been proposed based on ecology, biogeography, and phenotypic data (Waples 1991; Dizon *et al.* 1992; Vogler & DeSalle 1994; Legge *et al.* 1996), and although divergences in such characters are recognised as important parameters to define ESUs, it has also been suggested that the period of evolutionary time that populations have been isolated should be considered, and that their identification should be at least partially based on molecular genetic data (Avise & Ball 1990; Moritz 1994a).

The phylogenetic 'diagnosis' of separate ESUs currently advocates an operational definition which incorporates *reciprocal monophyly* of mitochondrial DNA (mtDNA) alleles, and *significant differences* in allele frequencies at nuclear loci. Using this approach, studies on the genetic structure of natural populations have been used to recognise or question ESUs for conservation

in many taxa, such as marsupials (Moritz *et al.* 1996), fur seals (Lento *et al.* 1997), fish (e.g. Riddle *et al.* 1998) and birds (e.g. Lovette *et al.* 1999; Tarr & Fleischer 1999; Zink *et al.* 2000).

However, reciprocal monophyly can in principle be due to the sharing of a single substitution (e.g. Hammond *et al.* 2001) and, in birds, sequence divergence between ESUs has so far been shown to vary between 1% and 8% (Avice & Walker 1998; Zink *et al.* 2000). Furthermore, using genetic distances has been shown to be suspect when comparing among populations, because there are indistinct boundaries between the levels of divergence observed within and among different taxonomic units in many groups. The use of single diagnosable characters to define ESUs (Vogler & DeSalle 1994) has been questioned because it then becomes essentially a typological method, which ignores evolutionary processes; such patterns can potentially become established very rapidly in genetically diverse populations due to fragmentation, genetic bottlenecks and drift. This can result in an extremely conservative interpretation, and the over-diagnosis of units for conservation. While conservative approaches to species conservation are potentially very valuable, in practice conservation managers may need to be given information that will assist in prioritisation of effort in future management scenarios, and over-diagnosis could therefore be regarded as counter-productive.

Importantly, however, there are also several examples where nuclear markers with high levels of polymorphism, such as microsatellites or MHC loci, have provided an alternative picture of population divergence from that offered by mtDNA (e.g. Pope *et al.* 1996; Hedrick & Parker 1998; Kirchman *et al.* 2000). ESUs have also been defined on the basis of reciprocal monophyly assessed solely from differences at microsatellite allele frequencies (Small *et al.* 1998; Parker *et al.* 1999). Recent studies on ESU designation in endangered species using mtDNA have advocated the use of microsatellites to corroborate results and establish precise management guidelines (Moritz 1994b; Waits *et al.* 1998; Manceau *et al.* 1999), and it is in this direction that avian studies need to go since they have been predominantly mitochondrial in the approach taken until now.

## CONSERVING DIVERSITY BELOW THE SPECIES LEVEL

### Population level management

Traditionally, genetic diversity below the species level has been described in taxonomic terms using mainly morphological characters, sometimes taking into account geographic isolation, and has mainly used the concepts of the

subspecies and/or race (they are often used interchangeably) and ecotype for the products of natural evolution, and landrace, breed or variety for the products of artificial selection. However, the definition of some of these descriptors varies greatly in the literature and there are many 'grey areas' where they overlap. The implicit assumption is that they encompass some cohesive and ultimately identifiable component of the genetic diversity found within a species. It is now becoming increasingly clear that we need to understand what these descriptors mean and what relevance they have for conservation, because the judicious management of these and other elements of intraspecific genetic diversity will become a key element of future conservation programmes in order to maintain evolutionary adaptability for the future. One problem with the taxonomy of subspecies, races and ecotypes, which have a variety of morphological and ecological definitions, is that although they may be operationally effective for taxonomists in the field or museum, they mostly lack any component which incorporates the evolutionary history of populations, whether they diverged in sympatry or allopatry, and how often they exchange genes now or did so in the past. For these reasons (and the more subjective argument that many modern subspecies were originally described more for arbitrary, geopolitical reasons rather than using sound taxonomic logic), their use has been called into question and molecular methods advocated (Ryder 1986).

The relationships between phylogenetic definitions of units for conservation such as the ESU (Ryder 1986) and the management unit (MU; Moritz 1994b) and traditional taxonomic descriptors such as the subspecies, race and ecotype are far from obvious. It is clear that many authors have in the past, and continue to, equate the ESU level with that of subspecies (e.g. Ball & Avise 1992; Zink *et al.* 2000) and indeed this was partly the original motivation for the ESU idea (Ryder 1986). However, ESUs, by many definitions, are automatically regarded as phylogenetic species and yet in some cases this division could, in principle, be applied from very recently derived subpopulations of the same species (e.g. in the Mariana crow; Tarr & Fleischer 1999). The concept of the management unit (MU) is now commonly in use to diagnose subdivided populations where divergence time has not been sufficient to accumulate evolutionarily distinct characters, or some other factor such as limited gene-flow has kept the populations genetically non-independent (Moritz 1994b).

### **Anthropogenic isolation**

A common problem facing practising conservation biologists centres on the management of recent and often anthropogenically isolated populations,

which may not, in many cases, be appropriately classed as ESUs (Tarr & Fleischer 1999). Such populations are often demographically inviable and may possess low amounts of genetic variation. In these cases, identification of the management unit may often be a more applicable approach (e.g. Britten *et al.* 1997; Baker *et al.* 1998; O’Ryan *et al.* 1998). Many of these studies are being carried out with the aim of identifying management units for translocating individuals to augment potentially demographically inviable populations (Moritz 1999). A major criterion identified by Moritz (1994b) for defining separate management units is the possession of significant haplotype frequency differences in mitochondrial DNA (although not necessarily at nuclear loci) regardless of the phylogenetic distinctiveness of the mitochondrial alleles.

Populations which have undergone rapid and radical changes in their habitat quality and quantity, which have a degree of isolation from other populations, and which are small, pose special problems when interpreting genetic data. Thus assignment of MU status needs to be carried out with caution. For example, the extreme demographic fluctuations which may be relatively common in small isolated populations are likely to result in genetic drift and/or inbreeding, thereby accentuating differences in allele frequency and resulting in the further loss of alleles (e.g. Saccheri *et al.* 1998, 1999). This may potentially result in the fixation of alleles that could be locally unique. It is common for isolated populations to possess no more than a few mitochondrial alleles, and many such populations may have suffered serious decline during the last 200 years. Genetic sampling of these populations may further lead to apparent differentiation among populations (e.g. Sjögren & Wyöni 1994). The genetic patterns often observed in endangered populations result from recent demographic events as opposed to longer-term divergence, potentially complicating translocation plans.

As an example, Barratt *et al.* (1999) found a large number of mitochondrial haplotypes, some of which were highly divergent, in small, isolated populations of the red squirrel in the United Kingdom. The frequencies of these alleles were also extremely different, with many populations only containing alleles unique to the data set. Phylogenetic analysis of the sequences revealed no geographically consistent pattern of diversity among haplotypes in different populations, either in the UK or in western Europe. However, the red squirrel is known to have been extremely common, widespread and continuously distributed across western Europe before deforestation for agriculture in the middle ages, and has been decimated following the introduction of the American grey squirrel in the nineteenth century. As a consequence many southern UK populations that are today extremely small and isolated have only been threatened for a few hundred years and may



indeed have exchanged genes with neighbouring mainland European populations prior to the flooding of the English Channel, *c.* 9000 BP.

Under the criterion of diagnosability (Vogler & DeSalle 1994) the red squirrel has many diagnosable ESUs (indeed, one might argue, many phylogenetic ‘species’) in the mitochondrial data set, and certainly each population would be considered a separate management unit under standard criteria. However in the absence of phylogenetic structure in the populations analysed, and with the strong possibility of a purely demographic explanation of the data, one might consider whether any of the populations even represent separate management units. For populations with large numbers of alleles, such alleles may be found due to long-term population stability, rapid generation time and/or large effective population sizes (Bromham *et al.* 1996; Li *et al.* 1996; Good *et al.* 1997). In these cases, population fragmentation and the subsampling of a diverse mitochondrial gene pool could rapidly produce significant allele frequency differences among populations (e.g. Cornuet & Luikart 1996), a pattern that carries no evolutionary signal.

Therefore, under the circumstances described above for small subpopulations that are essentially remnants of once large, continuous and diverse populations, significant allele frequency differences or even fixation of different alleles in mtDNA can, in principle, accumulate in relatively few generations. This may be a general problem in endangered birds and island populations (e.g. Mundy *et al.* 1997) and also when managing isolated populations of sedentary species formerly possessing large amounts of genetic variation. The genetic trends often observed suggest that where possible (and certainly in birds, with their elevated capacity for gene-flow) a conservative management strategy involves the use of larger, geographically neighbouring populations for augmentation of small, isolated populations. Further, because of the small amounts of time since the fragmentation of many populations, such augmentation would be expected to be unlikely to result in genetic incompatibility. This does not preclude the possibility that locally adapted phenotypic characters may have become fixed within smaller isolated populations, a potential problem that may sometimes be tested (Crandall *et al.* 2000). The role of demography as a complicating factor in designating genetic management units is potentially important (and, for example, it predominates in domesticated species), and its incorporation into criteria setting on a case-by-case basis is a necessity.

### **Small populations/endangered species**

Although the small population/*ex situ* conservation paradigm which dominated conservation biology in the 1980s and early 1990s was extremely

important in reviving conservation biology as a science (Frankel & Soulé 1981; Soulé 1986) it has often been justifiably criticised subsequently for (in general terms) under-emphasising the need to maintain viable habitats in the wild, failing to incorporate the importance of the causes of decline in larger populations and because many biologists believe that captive breeding, with its inevitable concentration on single species, has a relatively minor role to play in conservation. This has concomitantly led many biologists to question the role that small population processes play in species viability and how much effort it is worth expending to mitigate against them. The role of demographic and environmental stochasticity in population dynamics and persistence has been intensively studied by population ecologists since the 1960s, and has thus gained much credence. Demographic management of critically endangered populations either *in situ* or *ex situ* is known to be of fundamental importance for their survival (see Chapter 6). More controversial, however, is the role that genetic variation and its loss through drift and inbreeding have in population persistence, since although this issue has received much attention over the last 20 years, documented examples of the importance of drift and inbreeding to population survival are sparse. However, the recent study of Saccheri *et al.* (1998) linking heterozygosity with probability of subpopulation extinction in a metapopulation of Glanville fritillary (*Melitaea cinxia*) butterflies, followed closely by a study demonstrating that augmenting genetic variation in a threatened snake population reversed a long-term decline (Madsen *et al.* 1999), have revitalised the debate.

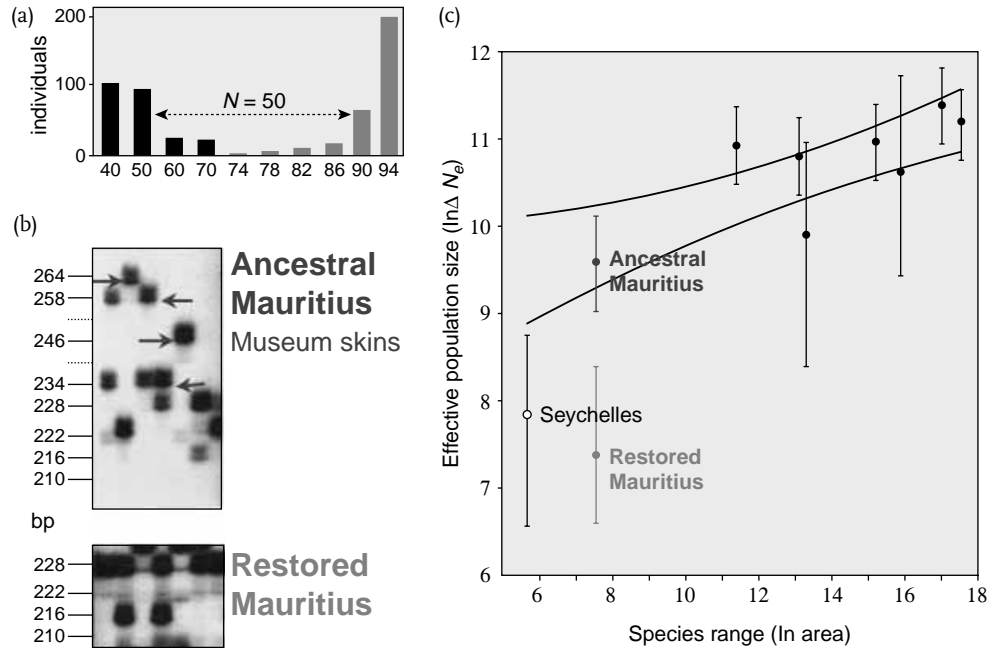
A long hiatus in studies of inbreeding and fitness at the level of the individual followed the first studies of avian inbreeding (in the great tit, *Parus major*) of Greenwood *et al.* in 1978 and van Noordwijk & Scharloo in 1981. However, the last ten years have seen the publication of several extremely important studies of inbreeding (and inbreeding depression) in birds, for both wild and captive populations. Many of these studies have explicitly applied molecular approaches to measure genetic diversity at the individual level (quantified, for example, by heterozygosity), within pedigrees or within small populations. Unsurprisingly, many studies have concerned island endemic species, a group which has suffered disproportionately from the effects of human intervention, and a group which is also expected to be least resilient in the face of environmental, demographic and genetic fluctuations (Frankham 1997).

In perhaps one of the most striking examples within a captive population, Brock & White (1992) convincingly demonstrated a causal relationship between genetic similarity of parents and inbreeding depression in

offspring in the critically endangered Puerto Rican parrot (*Amazona vittata*), a species that went through a bottleneck of 13 individuals, by correlating parental DNA fingerprint band-sharing coefficients with offspring inbreeding depression measured by reproductive output. Interestingly, unrelated Puerto Rican parrots had band-sharing coefficients similar to those of second-degree relatives of the closely related Hispaniolan parrot (*Amazona ventralis*), which did not go through such a severe bottleneck, and where inbreeding depression was not found to be as severe.

One of the most celebrated examples of a conservation success involving *ex situ* management in a bird is the Mauritius kestrel (*Falco punctatus*), which has recovered from a single wild breeding pair in 1974 to a wild population consisting of over 200 breeding pairs by 1990 (Fig. 1.2a). Groombridge *et al.* (2000) measured the loss of genetic variation resulting from the bottleneck using microsatellite markers typed for modern birds and museum skins up to 170 years old. Although extant individuals showed predicted low levels of diversity, variability in the museum skins was remarkably high (see Fig. 1.2b) and, when compared with the genetic diversity expected for continental kestrel species, was found to be of a similar magnitude for a species of its range (Fig. 1.2c). Interestingly, therefore, the Mauritius kestrel did not survive because of unsuspected additional genes in the wild population or because of a reduction of its genetic load due to a history of small population size, inbreeding and drift. In fact allelic diversity fell by 55% and heterozygosity by 57% during the bottleneck although allelic diversity probably fell by a much higher percentage since these estimates are much more sensitive to the limited sample available through museum specimens. The fact that this species recovered without augmentation suggests that it was only weakly affected by this bottleneck. The generality of this observation is, however, difficult to assess in the absence of temporal or spatial replicates. Its significance, especially given the fact that many island endemics remain in real threat of extinction, is that there may be no 'special case' for managing diversity in island endemics, and that although this population patently survived, many others may not without genetic management.

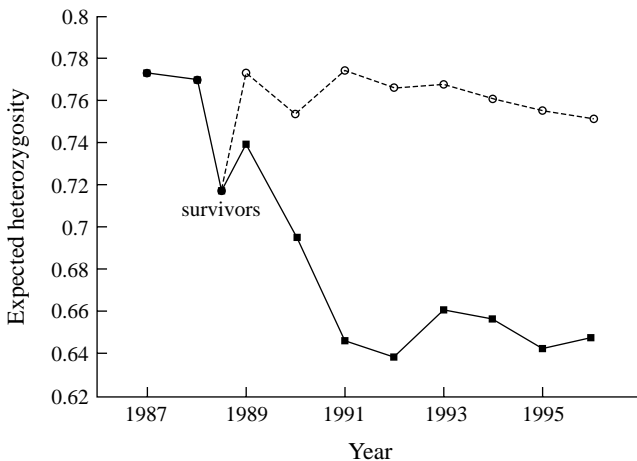
The genetic trajectories of natural bottlenecks in bird or other populations have rarely been documented, and in the absence of museum specimens, researchers are sometimes left with the signatures of such bottlenecks in the genes of present-day populations (Cornuet & Luikart 1996), but how often? The importance of the study of Mandarte Island song sparrows (*Melospiza melodia*) by Keller *et al.* (1994) is that the population



**Fig. 1.2.** Genetic diversity in ancestral Mauritius kestrels compared with modern continental kestrel populations; (a) demographic trajectory of the bottleneck; (b) genetic diversity using a microsatellite locus - arrowed bands are 'ghost' alleles unique to the ancestral samples; (c) relationship between relative effective population size and species range for a number of kestrel species. (Reprinted with permission from *Nature* (403, p. 616), 2000, Macmillan Magazines Limited, and the Senior author, Jim Groombridge.)

was followed through two bottlenecks in real time, so that real demographic data could be collected and, with the aid of a comprehensive pedigree of the island's small population, studbook estimates of inbreeding coefficients could be made. The consequence of this is that the genetic effects of the severe 1989 overwinter population crash, in which 95% of the population was killed, could be assessed. Inbred individuals were shown to have survived the crash with a much lower probability than non-inbred birds, and consequently this example has become one of the few convincing demonstrations of inbreeding depression in any wild population.

Subsequent analysis of the genetic trajectory of this bottleneck using molecular markers (Keller *et al.* 2001) has shown some striking results. Although, during the bottleneck, heterozygosity and allelic diversity were reduced similar to neutral theory expectation, these measures regained pre-bottleneck levels within two years of the crash, much faster than expected, so that a sample taken three years after the crash would show no evidence of the bottleneck having occurred, although average inbreeding did increase rapidly over this period. Low-level immigration (female arrived immediately after the storm) and genetic drift account for this recovery. Figure 1.3 shows the effect of immigration on expected heterozygosity. The descendents of crash survivors showed values reduced from 0.78 immediately before the crash to 0.64 five years after.



**Fig. 1.3.** The trajectory of average expected heterozygosity before, during and after the crash for all samples (open circles) and the subset excluding all immigrant lineages (closed squares). (From Keller *et al.* 2001.)

The role of inbreeding and drift in population and individual viability has been explored in as much, or perhaps more, detail in birds than in other vertebrates. However, as these examples and others show, much is still to be learned. More lessons need to be drawn from the many long-term studies of avian populations, for both endangered and stable species, and molecular studies on such populations are bound to be invaluable in highlighting new information.

## PERSPECTIVE

The quantification, characterisation and prioritisation for conservation of avian biodiversity at all levels will be key to how many species and populations survive the next 100 years, and in what condition. There is no doubt that to best conserve both present-day diversity and future evolutionary processes, the first priority must be to conserve as much habitat of as many different types as is politically possible, and the avian communities within them may then be able to play their role in ecosystem maintenance as they have done for over 100 million years. The decisions over precisely which regions are afforded protection are likely to be crucial in many cases, and presence or absence of certain avian taxa is likely to play a significant role in these choices, although whether they could or should dominate the conservation agenda over other taxa is questionable.

The continuing and seemingly insoluble debate regarding operational species concepts for conservation continues to hamper policy decisions and is in danger of creating a log jam for both legislation and practical management. Such problems have been most keenly felt in the United States where the interaction between the Endangered Species Act, ESU designation and subspecies-level conservation in particular, is giving rise to much debate (e.g. Zink *et al.* 2000). Such problems should serve to inform other countries and regions when considering the setting up of legislative apparatus for conservation of biodiversity.

Although seen as a somewhat esoteric exercise by those scientists concerned with protecting as much biodiversity as rapidly as possible, incorporating variation below the species into management programmes could in fact hold the key to effective conservation in the future. The preservation of adaptive processes and evolutionary potential needs to focus on populations and individuals since these are the currency of natural selection and hold the key to the future viability of all taxa. Management of subpopulations using genetic criteria, while desirable, is potentially fraught with inconsistencies, problems of interpretation and the tendency to over-diagnose units for

conservation or to follow guidelines too rigidly and without due regard to recent population demography. A pragmatic approach to interpreting and integrating genetic data in conservation, which takes into account both evolutionary 'signal' and demographic 'noise', but which is explicitly conservative when data are difficult to interpret (which they often are), may be needed in many cases. It is becoming clear that few, if any, 'hard and fast' rules can be used which are applicable to all situations and perhaps this is not surprising, given the myriad of evolutionary processes which can contribute the status of any given species, population or individual.